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THE TRANSPIRATION STREAM

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THE TRANSPIRATION STREAM

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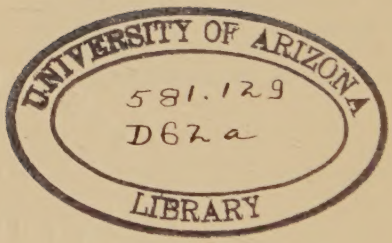
BEING A COURSE OF THREE LECTURES DELIVERED, ON THE INVITATION OF THE SENATE, BEFORE THE UNIVERSITY OF LONDON IN JANUARY 1924

LONDON
UNIVERSITY OF LONDON PRESS, LTD.
17 WARWICK SQUARE, E.C.4
1924



Printed in Great Britain for the UNIVERSITY OF LONDON PRESS, LTD.
by HAZELL, WATSON & VINEY, LD., London and Aylesbury.

PREFACE

THE following three lectures on *The Transpiration Stream* formed a short course delivered, at the invitation of the Senate, before the University of London in January 1924. In them I have endeavoured to indicate the present position of the Cohesion Theory of the Ascent of Sap, and have summarised the weightiest adverse criticisms of the theory and the rejoinders of its upholders, which have appeared since the publication of *Transpiration and the Ascent of Sap in Plants* in 1914. In the last lecture I have shown how, by an extension, this theory may, in addition to solving the old problem of the ascent of sap, be made to render a clue to the mechanism of the transport and the distribution of the organic substances in plants.

The discussion of the theory, as is often the case where an encroachment is made

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upon a vitalist position, has been always stimulating, if polemical. The evidence which is accumulating in favour of the extension of the theory to explain the transport of food materials is gathered from the researches of workers in very different branches of plant-physiology, and no doubt will be interpreted and evaluated differently by various minds. Clearly the touchstone will be experiment. Whether this theory stands or falls, physical facts call for a revision of our previous views on the subject.

A grant made from the Publications Fund of London University has made the publication of these lectures possible, and I desire to acknowledge my indebtedness to the Senate not only for making this grant but also for the interest it has evinced in my work.

HENRY H. DIXON.

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May, 1924.

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THE TRANSPIRATION STREAM

I

THE MECHANISM OF THE MOVEMENT OF WATER IN THE LIFELESS ELEMENTS OF PLANTS

I AM sanguine enough to hope that the majority of plant physiologists will soon agree that the recognition of the tensile strength of water affords a key to understanding the lifting of the sap in high trees.

It has elsewhere been pointed out that the peculiar structural characteristics of the wood of trees—the tissue in which the transpiration stream moves—are such that water partially or completely filling it, inevitably passes into a state of tension, when it is reduced in volume by abstraction from one or both ends. Under normal

circumstances abstraction of water is effected by the cells of the leaves in contact with the upper ends of the ramifications of the wood, and so the water coming from the lower parts of the plant is drawn up in a state of tension hanging from these upper terminations.

Naturally this hypothesis was submitted to rigorous criticism. Some of this was immediately more or less satisfactorily answered. The answers to some have been delayed. Some doubts possibly may have to await their answers long.

One of the most difficult antagonistic criticisms was the suggestion that possibly water in the wood is not normally continuous from the base of the plant upwards to the leaves. Generally when sections are cut of the wood of transpiring plants some of the tracheæ are found to contain gas, and some are filled with water. The proportion of those containing gas was variously estimated. Those containing even a small bubble are not available, for the stream raised by tension developed from

above. Evidently a very small proportion of tracheæ suitably distributed could thus break the continuity of the cohering stream of water.

Thus, although it might be pointed out that all the processes employed in making the preparations showing these bubbles, tended to increase their number, people very properly demanded definite evidence as to their presence and distribution in the intact plant. Striking evidence on this point has lately been forthcoming.

In 1915 Hans Holle found that even in leaves which had completely wilted from loss of water, intact water-columns may be microscopically observed in the vessels of the vascular bundles.

H. R. Bode in 1923 examined the stems and petioles of several rooted plants. He found that, even in the last stages of wilting, the water-contents of the tracheæ are continuous, and in no case are discontinuities or bubbles developed unless artificially introduced by wounding or by removal of the living cells in contact with the walls of the

tracheæ. He was able actually to measure the contraction of the water conduits due to the tension developed by loss of water. The original volume might be recovered when the lost water was restored.

Bode also showed how the usual methods of preparation introduced bubbles. His work establishes the continuity of the water-contents of the wood of herbaceous plants, and certainly it would be hard to maintain a different state of affairs in the tracheæ of woody plants without being open to the charge of special pleading.

Another doubt which has militated against the tension theory was the possibility that the tensile strength of water —though admittedly great—is not sufficient to secure the cohesion of the water-column, when the latter is exposed to the forces due to its own weight and to the resistance offered by the channel in which it moves.

Of all investigators Ursprung seems to have been most obsessed with this doubt. His criticisms are couched in the most

candid terms, and he does not hesitate to indicate what he thinks of those who arrive at different conclusions from his own. This gives a piquancy to his contributions to the literature of the subject which is absent from the work of other contributors.

From the first, Ursprung was displeased that appeal should be made to the cohesion of water. The fact that air is present dissolved in the water contained in the water-conduits precluded for him the significance of cohesion in the ascent of sap. It is touching to read his withering scorn of the unfortunate investigator who maintained that large quantities of dissolved air do not militate sensibly against its cohesion. He sets the whole array of continental physicists on one side and commiseratingly isolates on the other this experimenter who dared, and still dares, to maintain this fact. In the same way the crude methods of the same investigator for determining the tensile strength of water are described as being based on the veriest ignorance of the properties of matter and of the laws of

diffusion, and as giving outrageously high figures. The point of his rapier-criticism, however, is somewhat blunted by the knowledge that later Ursprung himself found that the estimates he condemned as excessive had to be raised more than 50 per cent, and that this greater cohesion was found in water certainly containing a considerable amount of air.

Here it is sufficient to state that experiments on fresh sap just as it is centrifuged from the water-conduits of a tree, without abstraction of dissolved gases, show that it is possessed of cohesion which is only overcome by a tension of about 200 atmospheres. This is a minor limit ; and it is pleasant to record that owing to the researches of Renner—and of Ursprung himself—it should probably be raised to 315 atm.

The method by which this higher figure for the tensile strength of water was obtained is very interesting.

The annulus of a fern-sporangium is a mechanism for using the cohesion of water

for the dissemination of the spores. The water enclosed in its cell-walls diminishes in volume by evaporation. The contracting water draws after it the cell-walls which adhere to it. This causes the thin outer wall of each cell of the annulus to collapse inwards, while the lateral and inner walls, being comparatively thick and rigid, are bent by the tension from the form of a U to that of a C. Ultimately so much water is lost that the stiff sides of the cell refuse to follow the water and a rupture in the latter is produced. On the instant the rigid sides are freed from the bending force and by their elasticity recover their original form. The jerk, communicated to the annulus by this recovery, fillips out some of the spores.

In this process it is evidently evaporation from the outer cell-walls which removes water from the cells. This only takes place when the vapour-pressure at these surfaces is greater than the vapour-pressure in the surrounding space, as evaporation proceeds the water surface in the

outer walls recedes into the substance of the walls, and the capillary forces developed in its menisci exert a traction on the fluid within the cell. This is resisted by the cohesion of the water, and the latter passes into a state of tension. Continued loss leads to more re-entrant menisci with smaller radii of curvature and greater tension. According to a well known law the vapour-pressure at a water-surface is reduced with its radius of curvature. Hence the loss of water from these menisci slows off the more re-entrant they become and the higher the tension in the water of the cell. At a certain surrounding vapour-pressure evaporation will cease and the tension will cease to rise. Under the conditions of dehiscence this state is not reached until after rupture has taken place. It is also well known that the vapour-pressure of a solution is a function of its osmotic pressure. Hence by suitable arrangements we may secure that the vapour-pressure of the water in the cells of the annulus at the moment of rupture

will be in equilibrium with the vapour-pressure over a solution of known osmotic pressure.

Utilising these considerations, Renner determined the tensile strength of the water in the annulus-cells as amounting to 300 atm. and in exceptional cases to 350 atm. His method consisted in observing the rupture of water in the annulus-cells enclosed in a small capsule where the vapour-pressure was controlled by the presence of a comparatively large quantity of a solution of known osmotic pressure. The balancing osmotic pressure was found by trial and error.

Using the same method, a tensile strength of about 315 atm. was recorded by Ursprung himself.

Two points noted by Renner may be of interest. The tensions at which rupture is observed show wide variations—about 80 atm. Similar variations recorded in my earlier measurements were very adversely criticised by Ursprung. J. Meyer's experiments also indicate similar variations.

A second point is of importance: these tensions were observed in water containing dissolved air. Renner does not believe its presence determined the rupture even at these tensions. With regard to this point Ursprung seems now silent. But he does not mention any precautions taken to eliminate the air in his experiments, and so, from the general conditions, we must assume its presence in his experiments also.

On the whole, this very ingenious work with the fern-annulus seems to have had an educating effect on Ursprung, for now he declares that the vital theory of the ascent of sap, for which he stands, does not exclude any one physical force—not even cohesion—from participating in raising the sap. This state of mind may be aptly described in Renner's words that now Ursprung is half-way on the road to Damascus.

Renner has also contributed very interesting work in determining the actual tensions developed in transpiring branches. Having fixed the lower end of a transpiring

woody branch in a potometer he artificially increased the resistance of its lower part either by clamps or by successive partial sections. The rate at which the branch drew up water was then observed. Next the leafy upper part of the branch was removed and attachment made to the upper part of the stump with an air-pump. Then the rate of upward flow for a given difference of pressure at the two ends of the stump was observed. Assuming, then, that the flow in each case is proportional to the difference of pressure, the difference of pressure above and below the resistance during transpiration may be calculated. Tensions of 10–20 atm. were obtained by this method.

These results were subjected to the usual spicy criticism by Ursprung, who maintains that under a constant difference of pressure at the opposite ends of a shoot maintained by a pump, the amount transmitted falls off as the length of the shoot is increased ; while, if this difference is maintained by the osmotic value of the leaf parenchyma,

so long as the axis is alive, the amount of water transported is not reduced with increasing length. The thesis is remarkable ; and in view of experimentally ascertained facts is untenable.

Nordhausen has also adversely criticised Renner's results. He lays great emphasis on the fact noticed by Renner that, when the leafy top is cut off from the experimental branch, the reduced gas-pressure and the strains set up by the previous transpiration in the stump of the branch left in the potometer continue to draw water upwards. This renders uncertain the exact value which should be set on the effectiveness of the difference of pressure produced at the two ends of the stump by the air-pump which was subsequently attached.

Nordhausen sought to improve Renner's method by comparing the flow generated by the tension developed by a branch with that of a known pressure-difference through an artificial resistance. The resistance was a cylinder of unglazed earthenware, 5 or

7.5 cm. long and having the same diameter as the wood of the branch. This was connected on to the base of the branch by a luting of plastic clay. The fineness of the clay, by supporting the menisci of bubbles formed, prevented, at least to some extent, ruptures spreading in the water between the upper surface of the resistance and the lower surface of the wood of the branch. By means of this ingenious contrivance he showed that transpiring branches developed tensions in the water just above the resistance amounting to 7–8 atm. Attaching his apparatus to various levels of trees in the open he found tensions amounting to 3–4 atm.

Although Nordhausen does not treat these figures as lower limits of the tensions developed in the water-conduits of trees, they most certainly are such. Renner pointed out that the plastic clay used in the luting will be drawn up into the tracheæ and tend to plug the lower end of the branch. This will increase the resistance of the base of the branch and hence reduce the flow

of water through the artificial resistance. Nordhausen sought to evaluate this error by experiment, and now allows an addition of 15 per cent on this account to the apparent flow through the resistance. From the nature of the case the effect of the resistance thus introduced will be irregular, and satisfactory allowance cannot be made for it. Renner also pointed out the difficulty introduced by the development of bubbles in the open tracheæ, as tension mounted, increasing to an unknown amount the resistance of the base of the branch.

But in Nordhausen's experiments two other important factors have, I think, been overlooked, which act to depress the observed tensions. First, in cutting the branch, whether under water or not, the continuity of the stretched water-columns is broken. How infallibly ruptures are started in this way is made clear by Bode's observations on the continuity of the water-columns in transparent organs. This experimenter found that a light touch of a metal point on the outside of a trachea

containing stretched water determined a rupture in the enclosed liquid. The rupture thus started will probably be visibly closed by the water-supply used to keep the wound wet, but the air liberated from the stretched liquid will adhere to the invisible particles in the supply and, however small the dimensions of the bubbles it forms, they will produce points of weakness in the water. As soon as the tension developed in the water above the resistance becomes greater than the surface-tension associated with the radius of curvature, these bubbles will increase in size and either fill the cavities of the opened tracheæ, and so increase the resistance of the lower end of the branch, or their surfaces may find support in the fine-grained particles of the plastic earth, and so resist the tension somewhat longer. It seems almost certain that the higher tensions observed by Nordhausen were by no means the breaking loads of the water at the base of the branch, nor the maximum tensions the leaves above can generate, but rather the tensions which

were required to overcome the surface-tensions of these bubbles.

The second factor, which tends to reduce Nordhausen's estimates of the tensions generated by transpiring branches, is the well-known progressive change which takes place at a cut surface of wood when transmitting a rapid water-supply. This unestimated and rapidly rising resistance should be added on to the artificial resistance interposed in the current.

These two neglected points act in Nordhausen's experiments, and, if it were possible to make proper allowances for them, would in all probability raise his results to figures as high as Renner's and in some cases possibly higher. At the same time it must be admitted that neither method does more than indicate high tensions. The absolute measurements obtained cannot be relied upon.

A very ingenious method of observing the immediate effect of these high tensions has lately been published by H. R. Bode. His apparatus consisted essentially of a potometer, the small reservoir of which was

provided with plane parallel transparent sides, so that microscopic observation of the included base of the branch was possible. This base previous to its insertion was ringed and stripped of its cortex, and its transverse cut surface was rendered impermeable with a coating of wax and cocoa-butter. By means of a horizontal microscope changes in the diameter of the ringed portion might be easily followed. Hourly readings of this microscope showed a progressive diminution of the diameter, as transpiration proceeded from the leafy top of the branch. A sudden return to the original diameter was observed when the leafy top was cut off with a shears. Evidently the tension developed by transpiration is responsible for the continuous contraction. When this tension is relieved by the cutting, the distorted wood-tissue leaps back to its original dimensions. Renner had previously observed this recoil (" Ruckstoss ") in potometer experiments and had quite rightly interpreted its meaning. However, his critics preferred to re-

gard the recoil as due to the distortion and recovery of the living cells. Bode's experiment seems to show the correctness of Renner's explanation. Furthermore, Bode was able to observe directly the distortion of individual tracheæ *in situ* when exposed to tension. I myself had some years ago pointed out that the inflection of the thin parts of the wall of spiral and annular vessels between the supports was a record of the tension now so generally admitted.

From the foregoing short summary of the work which has been done since 1914 on the physical condition of the water of the transpiration stream, it will be seen that the position of the cohesion theory has been materially strengthened: (1) by the observation of continuous water-columns in herbaceous plants even in the wilting condition; (2) by direct observation of the compression of the conducting tracts during transpiration, and (3) by the determination of a minor limit of 300 atm. for the tensile strength of water containing dissolved air.

II

THE FUNCTION OF THE LIVING ELEMENTS IN LIFTING THE WATER CURRENT

The importance of the rôle of the living elements in raising the transpiration current is rated very differently by various investigators.

Of all recent workers Sir Chunder Jagadis Bose assigns greatest importance to the special actions of living cells in the lifting of water in plants, and I shall now try to give a short description of his views and discuss very briefly his work in this connection. At the outset I may state that his general point of view is so remote from my own that I often find great difficulty in seeing the sequence of his arguments. It is written "As far as the east is from the west," and I may remind you I come from the comparatively far west. Bearing

this difference of point of view in mind, it seems most satisfactory to preface this consideration of Bose's work with a short outline of his theory in his own words. On page 94 of his book, *Physiology of the Ascent of Sap*, he says: "We are now in a position to trace a complete picture of the physiological mechanism of the Ascent of Sap throughout the length of the plant. The pulsatory activity is initiated in the root, effecting the absorption of water from the soil. Similar activity in the cortex pumps water up through the stem from cell to cell, and also injects water into the vascular tissue of the xylem along which it is physically transferred. The water conveyed by physiological conduction and physical convection reaches the leaf where it is distributed along the veins and their numerous ramifications and is eventually excreted or transpired into the intercellular spaces, whence it finds exit to the atmosphere outside by evaporation."

To establish this view, his line of argument appears to be as follows: He takes

two phenomena admittedly bound up with the vital actions of cells—these two are the movements of the leaves of Desmodium, and the growth of a growing point—and examines how they are modified by certain internal and external conditions. Then he labours to show that by exposure to the same conditions similar modifications are introduced into the ascent of sap. The comparison of the influence of each of these conditions on the three phenomena supplies him with "conclusive" proof that the movement of water in the ascent of sap is directly due to the vital actions of cells in the stem. This method of argument is pushed still further, and Bose is able, by the same mental process, to convince himself of the actual nature of the vital processes in the cells which are responsible for the ascent of sap. By his own observations and deductions he arrives at the conclusion that "the cells of the upper and lower halves of the pulvinule of the leaf of *Desmodium gyrans* execute alternate contractions." "The period of a complete pulsation varies

according to circumstances from a minute to four minutes or so" ; "in other words *rhythmic* activity is strongly developed in certain tissues." By means of his crescograph Bose has convinced himself that growing organs exhibit "an autonomous activity of a pulsatory nature." Accordingly, when he believes he has shown that the ascent of sap is modified in the same way "as these two typical instances of pulsatory activity" by variations of the physiological conditions, he finds no difficulty in formulating his theory more precisely, and declares that the ascent of sap is due to the pulsatory activity of certain cells in the stem. Indeed, each comparison of the influence of external and internal conditions on the three phenomena becomes for him, as he says, "a crucial proof that the maintenance of the ascent of sap is effected by the rhythmic activity of living cells."

In this summary I have used Bose's words wherever feasible in order to convey, if possible, to those of you who have not

had the advantage of reading his book, the peculiar verbal transitions which often form an essential part of his arguments. Here "alternate contractions," varying from one minute to four minutes or so, become "pulsations," and these glide easily into "rhythmic activity."

In order to examine the effect of the varying physiological conditions on the velocity of the ascent of sap, Bose has invented new methods. The idea of one was suggested by observing the manner in which a wilted plant often recovers when supplied with water. Bose figures a very remarkable instance. He supposes recovery to take place from below upwards, each leaf recovering and becoming erect as the rising water reaches it. On this assumption the velocity of upward movement may be determined by noting the time elapsing between the contact of the water with the base of the stem and the erectile recovery of the leaf. This latter movement he renders more perceptible by a magnifying lever recording on a horizon-

tally moving plate. For myself it is far from obvious that this method records the velocity of the ascent of sap, but the manner in which Bose uses it fairly takes one's breath away. By an astonishing transition, and without any explanation, he assumes that the rate of erection gives a measure of the velocity of the current, and by this means studies the effects of temperature, anæsthetics, and poisons on the rate of ascent.

He also employs an electrometric method depending upon his view that "the electric condition of a tissue undergoes a definite variation under changes of turgor; a *diminution* of turgor induces an electric change to galvanometric *negativity*, while an *increase* of turgor induces, on the other hand, an electric change to galvanometric *positivity*." "A plant under drought has its turgor diminished throughout its length. If now we make two electric contacts, A with the stem and B with a distant leaf, the electric conditions of the two points will be more or less similar.

Irrigation will, however, cause an ascent of sap, which will reach the lower contact A earlier, and induce an enhancement of turgor at that point. This will at once be signalled by a sudden electric change to positivity at A." To detect this electric change, Bose uses a quadrant electrometer. Strangely enough, he notices the fact that he found no difficulty in maintaining the electrification of the needle. He does not definitely record the sensitiveness which he used, but says it could be raised so as to give 1 mm. deflection for a difference of potential of 0.001 volt.

With Dr. J. H. J. Poole's assistance, I have tried to repeat Bose's method. Tested before and after the experiment, the instrument we used gave a deflection of 1 mm. for 0·004 volt. There was no change of zero during the experiment. Two plants were experimented upon—*Sparmannia africana* and *Pelargonium zonale*. The earth round both was dry; that round the latter was very dry; but neither showed any definite signs of wilting.

Fig. 1.—The results of the experiments described in the text are here graphically represented. For comparison a similar graphic record of one of Bose's experiments is shown below.

The plant of Sparmannia was first subjected to experiment. After the connection had been made, as Bose described, a slow movement of the spot of light occurred. A few minutes later the spot came to rest at 19·7 mm. to the left of zero (Fig. 1). This, as the instrument was arranged, indicated that the point A was positive relative to B. When observation showed that the spot was sensibly stationary, the earth in which the plant was growing was irrigated with water about 25° C. Immediately the spot moved to 17·0 mm. and slowly crept back to 19·3 mm. which it reached two minutes later. During the next thirty minutes it crept slowly to 21·0 mm. During all this time nothing like a to and fro motion, corresponding to Bose's pulsations, was observed, nor was there any sudden large deflection. Point A was 8 cm. above the surface of the soil. The temperature of the room was about 14° C.

The experiment with the geranium gave a similar result. After connections had been made the spot of light moved in three

minutes from 9·0 mm. to 12·6 mm. In the next seven minutes it returned to 11·5 mm. At this moment the plant was supplied with water at about 25° C. In the next minute the spot moved to 12·0 mm. and in two minutes more returned to 11·6 mm. From that time forwards, for the next forty-seven minutes, it crept slowly and uniformly to 22·3 mm. The experiment was then broken off. As before, the room temperature was about 14° C.

Certainly in our hands the experiment failed to give the results obtained by Bose.

I think I should also record my failure to obtain confirmation of a rhythmic change of potential in the cells of the stem by means of Bose's method of the electric probe. In this investigation I had the assistance of Mr. N. G. Ball. The electric probe which we used consisted of a platinum wire coated with celluloid and enclosed in a glass tube. The glass tube was fixed firmly in the body of a microscope, so that the sharp tip of the wire, from which the celluloid had been stripped, projecting from

the glass-tube, occupied the position of the objective. The body of the microscope was placed horizontally and the vertical stem of the experimental plant was firmly clamped to the stage. With this arrangement the point of the probe could be advanced gradually through the tissues of the stem by the action of the micrometer screw of the microscope. By means of mercury in the ensheathing glass tube connection was made between the probe and one pole of the galvanometer, while the other pole was connected with another platinum contact embedded in the tissue of a morbid leaf, as Bose recommends. The circuit was completed through the plant. As you know, with a circuit like this and using a very sensitive galvanometer, which gave a deflection of 1 mm. for a current of 10^{-10} ampere, Bose records that he found, when the probe had been advanced inwards to a certain distance from the surface, that the galvanometer showed alternate deflections in opposite directions. The period of this alternation

varied, according to circumstances, from 13·5 seconds to about three minutes. The amplitude of the vibrations varied between 10 mm. and 66 mm. Our galvanometer gave a deflection of 1 mm. for a current of 5×10^{-10} ampere, and consequently we should have obtained vibrations of 2 mm. to 13 mm. in amplitude. We used in these experiments two plants of *Pelargonium zonale*, one of *Chrysanthemum sinense* and one of *Impatiens sultani*.

In the first experiment the pelargonium was kept at about 13° C., in the subsequent experiments the plants were kept at 26°–28° C., and without doubt were passing a vigorous current of water upwards. The course of all the experiments was similar. The probe was first brought into contact with the surface of the stem. A slight disturbance was registered and the spot of light came to rest. The probe was then advanced 0·1 mm. and the galvanometer gave a kick, bringing the spot about 18 mm. to the right. The spot slowly regained its first position. After ten minutes the probe

was advanced another 0·1 mm. and again movement to the right occurred followed by a return to the original position. In this way the results of seven 0·1 mm. movements of the probe forward, with ten-minute intervals, were observed. Sometimes the kick at movement was more and sometimes less, and occasionally it was followed by one or two irregular movements, possibly due to the slight distortions and recovery of the penetrated tissues. In no case was any approach to a regular vibration observed at any level in the stem. Yet these stems at the moment were transmitting an upward water-current and should, if Bose's arguments and observations are to be relied upon, have produced, when the probe reached a certain level, quite perceptible vibrations indicating the pulsatory activity of the cells of the innermost layer of the cortex. In the experiments which we made, carried out as far as possible according to Bose's instructions, no such vibrations could be detected.

Until further descriptions enable us to

repeat his observations in transpiring plants I do not think we are called upon to discuss their bearing on the ascent of sap.

Bose's criticism on the views of others is equally unsatisfactory. He dismisses the possibility of the osmotic action of cells entering into the ascent of sap as an important factor, because osmotic actions are so slow compared with the velocity of the rise of sap. He never envisages the possibility that slow osmotic actions proceeding over the enormous surface of the upper terminations of the bundles might produce a comparatively rapid motion in the tracheæ. He declares that Strasburger's experiments on killed plants are no argument in favour of purely physical forces raising the sap, because the living cells above exert the lifting forces which are transmitted backwards through the killed tissues, and by this means raise the water. He thus unconsciously admits the substance of the cohesion theory.

As was mentioned in the last lecture, Ursprung holds that action of the cells in

the stem removes the resistance which the transpiration current would otherwise experience in its passage through the wood. Prior to 1914 I collected a considerable body of experimental evidence against Ursprung's arguments that the action of living cells in the stem is directly necessary in raising the current. One thing is certain, I did not convince him. It is needless now to go over this old controversy. It is sufficient to observe that time in the end extracts the truth even from the bitterest polemics.

Apparently with the idea of finding some vital mechanism whereby the resistance of the water-conduits was nullified, Ursprung and Blum carried out a number of plasmolytic researches on the cells in, and bordering on, the wood. They convinced themselves that the osmotic pressure determined in this way was on the whole higher in the upper regions of the plant than in those below. Suddenly, in 1915, this method of attack was dropped, for these two investigators realised that the osmotic pres-

sure of the solutions in these cells could only exert a traction on the adjacent water when the cell-walls were not tense. As soon as the cells are fully turgid their osmotic pressure is of course balanced by the tension in the cell-wall and is powerless to draw in water from outside. From that time onwards Ursprung changed his objective and began to try and ascertain the " suction-force " of the cells adjoining the water-conduits. He used de Vries' method, namely by finding the concentration which produces no change of volume in the cells under examination. The tissue containing the cells to be examined was excised and rapidly stored in liquid paraffin. Sections were cut from these tissues under, and mounted in, paraffin. Then their microscopic outline was traced and the paraffin replaced by a solution of cane sugar. The concentration, in which no change of size occurs, has an osmotic pressure equal to the suction-force of the cell. Considering the difficulty of determining changes in volume from inspection from one side only,

and of obtaining satisfactory contact between the solution and the cell, it is remarkable that Ursprung and Blum have obtained such concordant results. It is also difficult to see how it is that, when the excisions are being made and the sections are being prepared, the volume of the cell does not alter. For at that moment they must be surrounded with solutions not necessarily of the concentration balancing their suction-force. In spite of these and similar difficulties Ursprung and Blum recorded a large number of determinations of the suction-force of the cells of plants. Thus they find higher values in the cells of the mesophyll than in those of either the lower or upper epidermis. The cells of leaves at a high level were found to have a higher suction-force than those at a lower level. The same was recorded for the cells of the different tissues at different levels in the stem, and for those of the stem when compared with those of the root. To the last detail these investigators find a gradient in suction-force which it might be supposed

would account for a flow in the normal direction throughout the plant. One can only regret that such a desirable series of determinations rests on such a precarious method.

If subsequent investigation establish this gradient, I cannot see how it will support Ursprung's contention that the living cells remove the " dead " resistance of the wood. A cell exerting a suction-force adequate to raise the water to its own level, must of necessity by means of the same force resist the suction-force of a higher neighbour in drawing water to itself.

It is not only in the stem that living cells come into contact with the transpiration current. From the foregoing it does not appear probable that the cells in the stem directly participate in elevating the sap. The case is not so clear with regard to those cells of the leaves which intervene between the highest terminations of the woody tracts and the evaporating surfaces lining the intercellular spaces of the leaves.

For the sake of simplicity, we may dia-

grammatise the structure of the leaf so far as transpiration is concerned. Essentially the evaporating surface is the outer cell-wall of a cell which may be in direct contact with a trachea containing water. This water we know is continuous through other tracheæ from top to bottom of the plant. At first suppose the space adjacent to the outer cell-wall to be saturated with water-vapour, while a pressure from below supports the weight of the water-column in the tracheæ. The cell will assume a volume such that the osmotic pressure within will equal the tension in the wall, and the vapour-pressure of the water in the wall will equal the vapour-pressure in the surrounding space. In fact the cell will be fully turgid, and the vapour-pressure of the water in its wall will be the same as the vapour-pressure of a free surface of water. This vapour-pressure is in equilibrium with the vapour-pressure of the water in the vacuole acted on simultaneously by the osmotic pressure of the solutes and by the tension in the cell-wall (turgor). Under

these conditions there is no passage of water through the system. Now suppose the vapour-pressure above the surface of the cell to be reduced. Immediately water evaporates. The water-surface consequently retreats into the submicroscopic interstices of the cell-wall and thus, by the curvature of its menisci, tends to lower its own vapour-pressure. This reduced vapour-pressure of the water in the wall is no longer in equilibrium with that in the vacuole, and consequently some water from the latter passes into the wall. In this way the vapour-pressure of the water in the trachea finds itself superior to that in the vacuole and some passes from it into the vacuole. Thus reduction of the vapour-pressure above the surface of the cell leads to the passage of water through the system. Now suppose that the pressure supporting the column of water in the tracheæ is removed, evidently the hydrostatic head of the column will draw the menisci still deeper into the cell-wall so that the vapour-pressure of the water in the wall will be still further

reduced. This reduction may equalise it with the surrounding vapour-pressure, when the passage of water will come to a stop. It may reduce it below that of the surrounding space, when water will condense upon the cell and a downward current be established; or the reduction in vapour pressure may be insufficient to bring it down to the surrounding vapour-pressure. In that case the passage of water will still continue, but more slowly than before being loaded with, or pulled back by, the weight of the water-column. Evidently any resistance to the motion in the tracheæ will act to increase this backward pull, or tension, just in the same way as increasing its weight. Thus we can see that for any given tension in the leaf-tracheæ, there will be a balancing vapour-pressure in the leaf-spaces at which neither evaporation nor condensation will take place, and no passage of water through the plant will occur. If the vapour-pressure falls below this, upward motion begins; if it rises above it, condensation and downward motion ensue.

Another and possibly more simple way of envisaging the forces in the transpiring cells and adjacent tracheæ is to regard the solvent water throughout the system to be in tension, hanging from the menisci in the evaporating cell-walls. This tension is transmitted across the cells to the water-columns. The osmotic pressure of the solutes acting on the semipermeable membrane prevents these cells from collapsing, just as the spiral, annular, and reticulate thickenings support the thin-walled tracheæ.

So far as these considerations lead us, there appears to be no need of the intervention of vital cell-processes. An inanimate colloid cell provided with an inanimate semipermeable lining might be supposed to act in a perfectly similar manner. No doubt this simple theory of transpiration has many attractions, and may be found adequate under many conditions. Renner, who has gone into it elaborately from the theoretical point of view, appears to be satisfied with it.

Elsewhere I have pointed out that there

is a good deal of experimental evidence that the process is not quite so simple. (1) Experiments indicating that water continues to rise in cut stems of plants when their leaves are surrounded with a saturated atmosphere; (2) the inadequacy of dead leaves to draw up water; and (3) the phenomena of the raising of water in coenocytic fungi, all seem to point out that under certain circumstances, at least, vital actions in the transpiring cells are responsible for absorbing water on one side of the cell and for emitting it on the other, where it evaporates into the intercellular spaces. In such cases the energy for bringing the water to the evaporating surfaces would not be due to the inflow of heat there, but would be due to solar energy stored in organic substances and liberated by respiration.

Molisch's observation, that carbohydrates are used up quickly during rapid transpiration, seems to support this view.

On the other hand, a simple physical explanation for the arrest of transpiration

in dead leaves may be found. For example, the internal osmotic pressure of the cell keeping the cell-wall distended during life may reduce the resistance of the water-stream between the evaporating surface and the tracheæ. On killing, this tension in the cell-wall is relieved, and the cellulose micellæ may come closer together, thus increasing the resistance to the water moving into, and out of, the cells.

III

THE RÔLE OF THE TRANSPIRATION CURRENT IN THE TRANSPORT OF SUBSTANCES THROUGHOUT THE PLANT

In the two former lectures I have tried to show that the cohesion theory furnishes an adequate explanation as to how water is raised from the ground to the top of high trees. In this last lecture I shall endeavour to explain how it, not only thus furnishes the mechanism for the upward movement of water, but also supplies the key for understanding the general transport of substances in plants, whether this conveyance is in an upward or in a downward direction.

It is generally the transport of dissolved mineral substances upwards in plants which is emphasised as being the special function of the transpiration current. As soon,

however, as Fischer's observations, and those of others, established the presence of carbohydrates in the water filling the tracheæ, it became quite evident that these channels are effective in conveying organic substances as well as inorganic. These observations were extended by Schroeder and Wotchal, who showed that this water also contained proteins and enzymes.

The importance of the tracheæ in conveying organic substances has been questioned by some investigators. These authors are impressed with the fact that the buds, above a ring removing the cortex and bast of a stem, fail to develop if the amount of store-material above the ring is inconsiderable. This experiment is taken by them to establish the function of the bast in the conveyance of organic substances. Strasburger has already pointed out that this interpretation rests upon the fallacy of supposing that the removal of the bark as far as the cambium leaves the wood uninjured. As a matter of fact microscopic examination of the wood, thus

stripped of the outer tissues, shows that its tracheæ soon become blocked with air-bubbles and with gelatinous substances, generally assumed to be the degradation products from the neighbouring cells. The introduction of air-bubbles, when the adjacent cells are injured, has been also recorded by Bode. In these experiments colloidal substances—whether degradation products or not—accumulate in the tracheæ and of course may be expected to preclude the upward passage of all complex organic substances on their way to the developing buds. In this connection an observation, repeated several times last year, is of interest. When ringed Salix or Populus branches are kept in a moist atmosphere, a growth of callus slowly covers over the ring. The buds which fail to develop, as long as the ring is uncovered, develop immediately it is covered with callus. This may be interpreted in terms of our theory by supposing that the new cells of the callus either enable the water columns in the outer wood to be re-established, or else

they may render the colloid deposits in the tracheæ soluble. Possibly they discharge both functions. Miscroscopic examination of the callus establishes the complete absence of bast-tissue.

Taking all the evidence into account, we may conclude with certainty that the rising water-current conveys upwards not only dissolved inorganic substances, but that it is of importance in transferring organic substances also from the lower parts of the plant to its upper extremities.

Carbohydrates most certainly, and proteins very probably, are primarily manufactured in the leaves. Hence, in the first place, after formation they must be transported downwards from the leaves.

I think it is fair to say, that up to a few years ago, all orthodox botanists held that this primary transport was effected in the bast.

Czapek, in 1897, reviewed the evidence for this belief, and, adding several observations of his own, reported favourably on the established creed ; but he, like others,

never fairly considered the forces required to move these substances in channels formed of very narrow capillary tubes, with frequent cross-partitions and filled with viscid colloidal substances.

Many of Czapek's observations and deductions were adversely criticised by Deleano; and the latter experimenter obtained some striking evidence in favour of the conclusion that the intervention of living elements is not required for the transport downwards of the organic materials formed in the leaves.

The physical unsuitability of the tubes of the bast for the transport of organic substances, and Deleano's experiments showing that lifeless elements may transmit a current carrying these materials, would naturally indicate the tracheæ of the wood as the channel for these substances in their motion downwards as well as upwards.

This surmise is strengthened when we estimate the velocity necessary for the transporting current, if it is assumed to

pass in the bast. For this calculation we have only to measure (1) the cross-section of the bast available for the transmission of the current; (2) the volume of liquid transmitted, and (3) the time available for transmission. The necessary measurements are easily carried out on a potato-plant. A slender branch attaches the developing tubers to the assimilating plant. Vascular bundles pass down these branches from the plant to the tubers. To take an example, a selected tuber weighed 210 g. The total cross-section of the bast in the slender branch was 0·0042 cm.^{2}—this is a maximum measurement. Nothing is allowed for the thickness of the cell-walls. In about a hundred days all the material of the tuber must have passed this cross-section. According to analysis 24 per cent of a potato is combustible. Therefore more than 50 g. of carbohydrates passed through this conduit. Assuming the average concentration of dissolved carbohydrate to be 10 per cent, the volume necessary to convey 50 g. must have

been 500 cc. and its velocity must have been $\frac{500}{0{\cdot}0042 \times 100 \times 24}$, i.e. nearly 50 cm. per hour.

It is improbable that the concentration is ever more than 5 per cent. The concentration of bleeding sap seems never greater than 4 per cent. Hence it would seem right to raise even this figure to about 110 cm. per hour.

Again, we may make the calculation in a different manner. The amount of carbohydrate manufactured per square metre of leaf-surface per hour has been determined by many investigators. Brown and Morris found that a square metre of leaf of *Tropæolum majus* manufactured 0·24 g.[1] of carbohydrate per hour. Therefore a leaf having a surface of 46 cm.[2] may form in ten hours sunshine 0·011 g. of carbohydrate. Supposing one-third of this is used *in situ* for respiration,

[1] The estimate given in my address to section K (Botany) British Association, 1922, was based on an earlier, higher figure. It was also erroneous owing to an arithmetical mistake.

0·0074 g. must be transported from the leaf in twenty-four hours. The volume containing this carbohydrate (again assuming a concentration of 10 per cent) will be 0·074 cm^3. The cross-section of the bast of such a leaf has been found to be about 0·0009 $cm.^2$, therefore the velocity of the flow, if the bast is used as the channel of transport, must be $\frac{0{\cdot}074}{0{\cdot}0009 \times 24}$ or about 3·5 cm. per hour. Here, again, allowing for the thickness of the walls of the bast and for a more probable concentration, we should have to double this figure.

A flow of these velocities in the bast is quite impossible.

Realisation of the volume of the solution, which has to be transported, and of the velocity of flow which this necessitates, naturally drives one to consider if the open capillaries of the wood may not be utilised as channels of transport.

The emphasis, which has been laid on the function of the wood as providing a channel for the upward movement of

water, usually obscures the part it plays as a downward and backward channel also. Early experimenters, however, realised that under certain circumstances the current in the wood may be reversed. Hales quotes several experiments proving this point. He showed that when water is applied to a cut surface at the upper end of a branch it is drawn back into the branch and makes good the transpiration of its leaves. A tree inarched into two adjacent trees may continue to grow even after its own connection with the soil has been severed, drawing its supplies from its neighbours. Finally, a forked branch cut from a tree will remain fresh and continue to transpire water for many days if one limb of the fork with its leaves is immersed in water.

By means of an eosin-solution this reversal of the transpiration-current may be easily demonstrated. If the tip of an upper leaf of a potato-plant is cut under an eosin-solution the coloured liquid is quickly drawn back into the tracheæ of the conducting tracts of the leaf. From there it

passes into those of the petiole and makes its way not only into the upper branches and leaves, but also passing down the supporting stem, may completely inject the tracheæ of the tuber. From thence it may pass up into the wood of the remaining haulms of the plant. Its passage is entirely in the tracheæ of the wood of the conducting tracts.

Another very striking experiment may be carried out with the imparipinnate leaf of *Sambucus nigra*. Its petiole is split longitudinally for a few centimetres and one half removed. The remaining half is set in a solution of eosin. Then the solution is rapidly drawn up the wood-capillaries of the intact half-petiole, and soon appears in the veins of the pinnæ on the same side of the leaf, beginning with the lowest and gradually working up into the upper ones. Finally it appears in the terminal pinna. All this while the veins of the pinnæ on the other side of the leaf remain uncoloured. Now, however, the eosin begins to debouch into the base of the uppermost of these

pinnæ and spreads through its veins. From there it makes its way down the offside of the rachis to the bases of the lower pinnæ and from thence spreads into their veins. In this case we see very clearly how transpiration actuates an upward current on one side and a downward movement on the other. It is interesting to note that, if the terminal pinna and its stalk are removed, the eosin does not appear in the pinnæ of the offside, or only after a considerable time, when the small anastomosing conducting tracts of the rachis are utilised.

Louise Birch-Hirschfeld also has recently described many experiments with herbaceous and woody plants, tracing the path of the reversed current by means of lithium nitrate and eosin.

The cohesion-theory provides a ready explanation of these reversals. Transpiration, by drawing off water from the tracheæ, causes the water filling these tracheæ to pass into a state of tension. This tension determines a flow from any source wherever situated, and the continued

transpiration from the leaves draws the supply through the plant along the channels of least resistance. Hence it is that, if the cut vein of a lateral pinna provides the point of entry, the solution may pass backwards into the opened tracheæ. The injected tracts bring the solution down the rachis and petiole into the stem, while a few, or many, as the case may be, remain filled with colourless liquid, presumably the sap which is being drawn upward to supply the transpiring surfaces of the leaf. Generally the coloured liquid descends an appreciable distance in the tracheæ of the stem, before it begins to rise in the ascending current mounting to other transpiring leaves. As a rule, after some time—depending on the rate of transpiration and the amount of water supplied by the roots—the presence of the coloured liquid may be observed in certain continuous series, or filaments, of tracheæ in several of the conducting tracts of the lower parts of the stem. Similarly, if tubers or rhizomes are present, examination of these parts, after

a suitable interval, will show that many of their filaments of tracheæ are injected. Meanwhile the parts above the supplying leaf become coloured and it will be seen that the distribution of the coloured tracheæ is decided by the anatomical connections of those filaments of tracheæ which directly convey the coloured liquid from the point of supply through the petiole to the stem. In tracing the course of the solution, one is impressed with the fact that the path of least resistance is by no means always the shortest path in the wood. Transverse motion across several tracheæ seldom occurs, and the separate linear series of conducting tracheæ are practically isolated from each other laterally. This is what we might expect, bearing in mind Strasburger's experiments, showing the very great resistance offered to the flow of water in a transverse direction in the wood of trees. This isolation of the separate filaments of tracheæ in the leaf and in the stem enables the tension developed by the transpiring cells of the leaves, while it raises a water-

column in one series of tracheæ, to draw down a solution in a neighbouring filament of tracheæ terminating above in some local supply. If the anatomical connection of the two series is located in a subterranean organ the tracheæ of that organ may become filled from the supply.

Evidence, such as the foregoing, of the reversed stream in the water-conducting tracts is open to the criticism that the reversal may be due to the artificial conditions established in order to demonstrate the flow. Fortunately there is also evidence that reversals of the transpiration-current normally occur in uninjured plants. Recent work on the transmission of stimuli seems to indicate that these reversals are of frequent occurrence in normally growing plants—and incidentally shows that in many cases, at least, the wood of plants takes on the function of the nerves of animals.

The most striking evidence of this kind is afforded by Ricca's work on Mimosa. The transference of stimulus occurs in

Mimosa both in the basipetal and apical directions. Ricca has shown that this transference is due to the transport of a hormone from the point of stimulation to the responding region. His experiments also show that this substance is transmitted, dissolved, or dispersed, in the water which travels in the tracheæ; further, that it moves most rapidly towards those leaves which are transpiring most vigorously. Hence it is evident that the hormone is carried in the transpiration stream, and, inasmuch as the hormone often moves in a basipetal direction, it is evident that the water-current in the intact plant must often move in that direction.

The transference of phototropic, thigmotropic and geotropic stimuli has been shown by the important work of Boysen-Jensen, Paal, Stark, and Snow to be also effected by the transport of hormones. The velocity at which the stimulus travels is in every case from 10–100 times, or more, greater than the velocity of diffusion. The conclusion seems irresistible that for these

responses, just like that in Mimosa, the tracheæ of the vascular bundles transport the hormones in their transpiration stream. As is well known, this transport is often in a basipetal direction, and hence we have, in these cases again, examples of the reversal of the transpiration stream in uninjured plants.

It is reasonable to suppose that this downward current is able to carry organic food-substances as well as hormones.

Generally, in those parts which connect the manufacturing leaves with the storage-organs provision must be made, not only for transporting the substances back from the leaves, but also for the conveyance upwards of the water to supply the transpiration of the leaves. Hence the presence of the tracheal tissues is not direct evidence as to whether it is their function to convey one or both of these streams. In some seeds the case is different. In them a storage-organ is attached to the growing embryo. In the earliest stages the embryo derives all its nutrition in the form of organic

foodstuffs from the seed. There is no separate supply of water and hence no need for a separate channel. Later on, while this organic supply is still maintained, the embryo develops roots, which make connection with the water of the soil and convey water upwards directly to the embryo to cover the transpiration of its growing leaves. Here then, in the part connecting the storage-organ and the young embryo, there is a conduit or channel simply and solely for conveying organic foodstuffs and not concerned with transpiration. If the tracheal tissues are to provide for the conveyance of the transpiration stream and are not directly concerned in the transport of organic foodstuffs, then in these parts there would be no need for their development, while if they are the normal channels for this organic transport we would expect their formation. On the other hand, if the bast is the tissue responsible for the transport of organic substances, we would expect a specially large development of sieve-tubes and companion-cells

in these organs through which so much organic materials have to be conveyed. In that case little or no tracheal tissue would be required. Examination then of such connecting parts seems almost a crucial test of this theory.

I selected the germinating seeds of Lodoicea and Phœnix for this examination. I found that in the vascular bundles passing down the connection—in these cases the petiole of the cotyledon—there is a perfectly normal development of tracheal tissue. It appears neither rudimentary nor degenerate. Its normal development is quite consistent with the view that this tissue normally transmits a stream carrying organic food-stuffs, but is inexplicable if its function is to transmit only water and dissolved salts. The bast is normally, but not specially, developed.

The evidence which I have here summarised seems to me convincing that there is, as well as an upward current in the tracheæ of the wood, a backward flow of water, and that the transport of both

organic and inorganic substances is effected in these currents.

With regard to the mechanism by which these organic substances are introduced into the backward stream we have as yet no direct information.

No matter what view we hold as to the channels of transport, it is necessary to assume either active secretion in the protoplasmic lining of the assimilating cells, or occasional changes in its permeability, to allow of the exit of the manufactured organic substances. Direct evidence for the secretion of these substances into the conducting tracts would be difficult to obtain, but very complete permeability is indicated by the presence of proteins and enzymes in the tracheæ observed by Schroeder and Wotchal. Considerable changes in permeability are generally assumed in the case of all cells, and definite indication of such changes may be obtained in leaf-cells in the following way : by means of a special apparatus, which I need not describe here, the electrical resistance of a

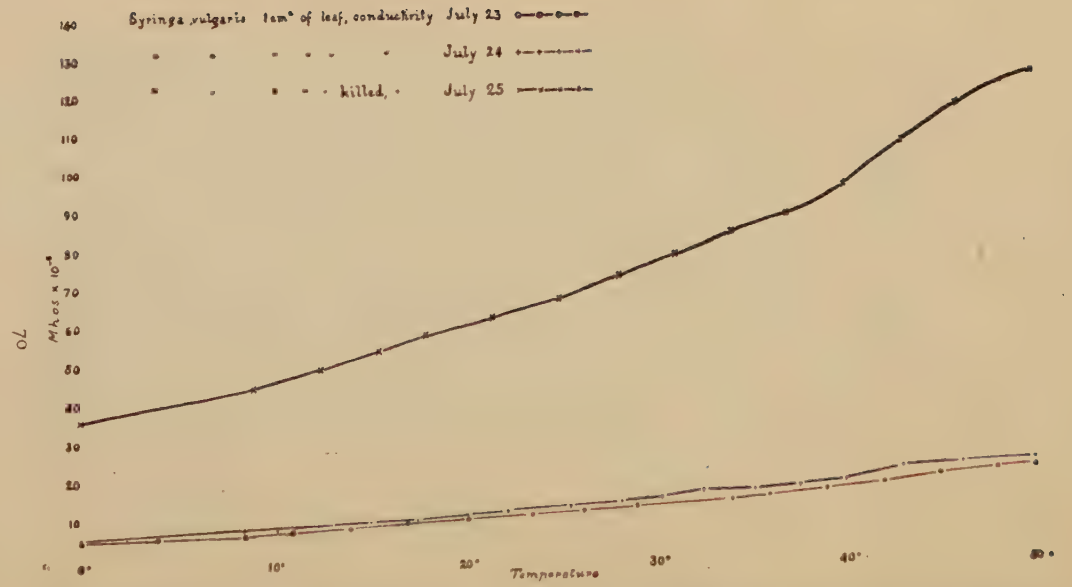

Fig. 2.—The two lower lines indicate the rise of permeability with rise of temperature of the cells of a leaf in two successive experiments. The uppermost unbroken line shows the permeability of the same tissue through the same range after it had been killed.

square centimetre cut from a living leaf can be measured at different temperatures from 0° to 50° C. Osterhout has given good reasons showing how changes in the conductivity of tissues give a direct measure of the permeability of their constituent cells. The resistance of the leaf-square is found to fall with the temperature-rise. Thus at 30° C. the conductivity, i.e. permeability, is about twice that at 10° C. (Fig. 2). Supposing then temperature differences in different leaf-areas, such as might well arise owing to differences of insolation, etc., it is evident that, when the tension developed in the adjacent tracheæ reaches a certain figure, it will draw the sap back out of the more permeable cells, while the continued transpiration from the cells round the terminations of other tracheal series will drag the sap still farther downwards. Changes of temperature are probably neither the only nor the most effective factors in altering the permeability of cells.

We can support this theory experimentally by artificially increasing the per-

meability of a selected leaf-region of a transpiring plant. If one of the pinnæ of a leaf of Sambucus be introduced through a split cork into a test-tube containing a little toluene, the vapour of the latter quickly renders the cells of the pinna permeable. At the same time under its action a brown pigment develops in their cell-sap. Afterwards the backward passage of the brown liquid drawn from these cells may be microscopically traced in the tracheæ of the rachis for a considerable distance.

In the same way an external gas-pressure, exerted on leaves previously rendered permeable by exposure to toluene-vapour, forces back into the tracheæ the contents of the vacuoles of the mesophyll. It can be shown that this liquid passing through the tracheæ contains carbohydrates.

The permeable cells thus more or less emptied of their contents must diminish in volume. Hence the volume changes in the leaves of transpiring plants recorded by Thoday fit in with this theory very

well. He found volume-changes amounting to a 7 per cent change in ten minutes. The introduction of a volume of liquid at the upper ends of the tracheæ would produce a very considerable downward displacement in the comparatively narrow strands of tracheæ supplying the leaf. Suitable measurements and calculations, kindly made for me by Mr. N. G. Ball, show that a 1 per cent contraction of a leaf might lead to a downward movement in the petiole of 16–45 cm. in the leaves measured.

We thus come to regard the wood as a specialised reservoir of liquid food-stuffs within the plant. Abstraction of water by transpiration sets up tension in its contents, while stability is conferred upon them by its subdivided structure. This tension leads generally to a flow from the supply in the soil to the exit in the leaves; but it also necessitates motion from any source towards any sink. Maintenance of the large and diffuse living body of the plant requires a large surface of interchange between the living body and this reservoir.

This large surface is provided by (1) the bast, (2) the tongue-like medullary rays penetrating into the wood, and (3) their extensions, the wood-parenchyma, intermingled with the tracheids and surrounding the vessels. These tissues are not only charged with the functions of introducing substances into this reservoir and of abstracting materials from the currents which pass in it, but also are most probably responsible for the duty of keeping the tracheæ viable by removing precipitates and coagulations and by preventing the formation of gels. Possibly this latter function, namely the formation, temporary storage and secretion of enzymes, may be assigned to the companion-cells and sieve-tubes of the bast. This zymogenic function of the bast is strongly indicated by its large development in the digestive haustoria of palm-seedlings, and by the clogging of the wood in ringed regions. The almost invariable association of wood with bast in the organs of plants finds a ready explanation on this hypothesis.

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Printed in Great Britain for the UNIVERSITY OF LONDON PRESS, LTD., by HAZELL, WATSON & VINEY, LD., London and Aylesbury.

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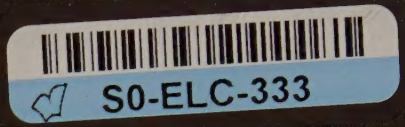
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